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Living Boundaries: Tracking Weed Seed Movement with Nondormant Seed

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Synthetic seed banks are a useful tool for tracking how weed populations change over time. By sowing a known number of seeds of a given species within a quadrat with defined boundaries, an investigator can measure the number remaining and thereby calculate demographic rates (e.g., mortality). The alternative is to use in situ seeds and estimate their initial population density via sampling. To make a synthetic seed bank approach useful within an agricultural system subjected to soil disturbances such as tillage, one would need a way to account for seeds leaving the initial quadrat (i.e., a way to follow how the area encompassing the sown seeds changes over time). Without accounting for the change in location/extent of the synthetic seed bank, any field operation moving soil will create additional uncertainty in population size. Depending on the "aggressiveness" of specific field operations and the initial size of the quadrat, this effect might be negligible or so large as to be intractable. Here, we describe a method for following a synthetic seed bank over time using a "living boundary" of nondormant seeds, which effectively play the role of tracers used in the study of dynamics in other scientific disciplines. Study quadrats in East Lansing, MI, and Arlington, WI, were sown with giant foxtail and velvetleaf at a rate of 2,000 seeds m^{-2}. The study quadrats were marked on the perimeter and diagonals using nondormant seeds of three marker species: kale, radish, and rye. The areas were then subjected to tillage and planting operations. Spatial coordinates of seedling locations for the marker and weed species were obtained through digital image processing. A nonparametric comparison of the spatial displacement of marker and weed species indicated that their empirical spatial distributions did not differ. The marker species quadrats described by the 50th, 90th, and 99th quantiles of movement contained all velvetleaf seedlings in Wisconsin, all velvetleaf seedlings in Michigan, and all giant foxtail seedlings in Michigan, respectively. The results suggest a simple rule for applying the method to field demography studies: after the original quadrat is deformed and seedlings have emerged, flag the polygon containing all marker seedlings to obtain the expanded quadrat containing the study weed population.

Nomenclature: Giant foxtail, *Setaria faberi* Herrm.; velvetleaf, *Abutilon theophrasti* Medik.; kale, *Brassica oleracea* L.; radish, *Raphanus sativus* L.; rye, *Secale cereale* L.

Key words: Field demography, synthetic seed bank, spatial distribution, quantiles of movement, Kolmogorov-Smirnov, nonparametric, convex hull, pulse-chase, population dynamics, spatial dynamics, demographic rates.

Synthetic weed seed banks can be a useful tool for studying the effects of management on changes in weed population size. Estimates of weed seed population density based on samples taken from the ambient soil seed bank are prone to high levels of sampling error due to the spatial patchiness of soil seed banks (Ambrosio et al. 1997; Cardina and Sparrow 1996). In contrast, synthetic seed banks start with a known number of seeds, and can thereby reduce uncertainty associated with the estimation of seed population density. The basic procedure for creating synthetic seed banks is to collect a large initial batch of weed seeds, assay its viability, and sow a known number of seeds within a defined area. Depending upon the goals of the study, one may maintain more or less control over the seed bank.

Detailed studies of recruitment dynamics that include realistic seed-soil contact can use a "seeded cores" approach (Teo-Sherell et al. 1996), in which weed seeds are mixed into a small volume of soil, which is then left undisturbed throughout the germination period, and recovered by extracting a larger volume of soil surrounding the seeded core. It is also common to place seeds within some sort of container that confines seeds to a known area (e.g., enclosure in mesh bags, buried pots or inverted glass jars filled with sand) (Telewski and Zeevart 2002). Every method constraining the movement or environment of introduced seed involves simultaneous creation of an artificial situation; one that may or may not cause a change in the behavior of the seed.

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Another approach with somewhat more realism involves measuring the components of the life cycle while mimicking agronomic management operations, such as tillage, manually. For example, Davis et al. (2004) examined the impacts of green manure and tillage on giant foxtail demography by placing foxtail seeds within seed banks bounded by large-diameter polyvinyl chloride (PVC) pipes, which were removed from the field when tillage, green manure incorporation, and planting took place to keep the seed banks from being dispersed. Tillage was simulated within the seed banks by hand mixing the seed and soil mixture. This approach kept measurement precision reasonably high, but relied upon the assumption that the simulated treatments did not influence the fate of seeds if compared to a hypothetical in situ population.

A still greater level of realism can be obtained in demographic studies where field operations are applied to an introduced/synthetic weed population without any artificial boundaries. One example of this approach is the work of Westerman et al. (2005), in which weed seeds were applied to a 3-m^2 quadrat nested within a larger 49-m^2 quadrat, with tillage, planting, and weed management operations proceeding as usual. While highly realistic in agronomic terms, this study may have also been subject to a large decrease in precision, since the odds of finding study individuals greatly decreases when they are manipulated without boundaries.

Here, we describe the results of an investigation into the use of such a synthetic seed bank method that aims for high realism while attempting to maintain the precision that is lost from the use of an unbounded system. In essence, the approach uses seeds of nondormant crop species as an ecological "tracer" to follow changes in the boundaries of

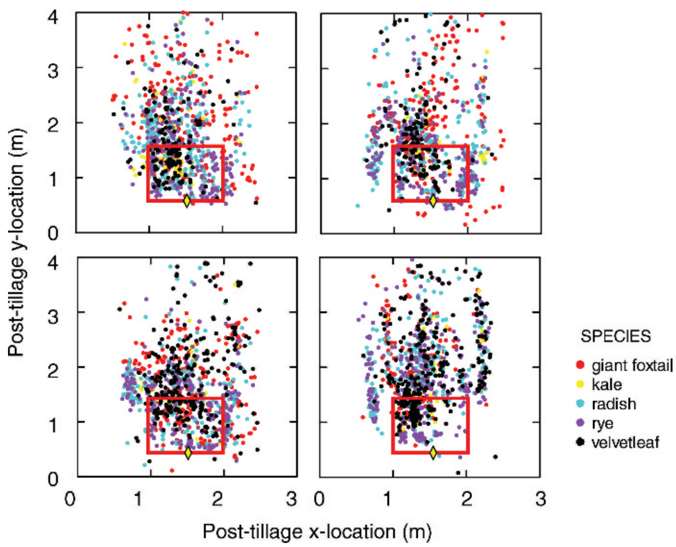

Figure 1. Digitized locations of synthetic seed bank species in East Lansing, MI, April 2004, for all replications (replications 1 and 2, from left to right on top; replications 3 and 4, from left to right on bottom). Red rectangle indicates location of original 1-m^2 quadrat, whereas graph frame indicates relative position of expanded quadrat. Yellow diamond indicates origin of 1-m^2 quadrat, from which spatial displacement calculations were made. Tillage was performed perpendicular to the x-direction and parallel to the y-direction.

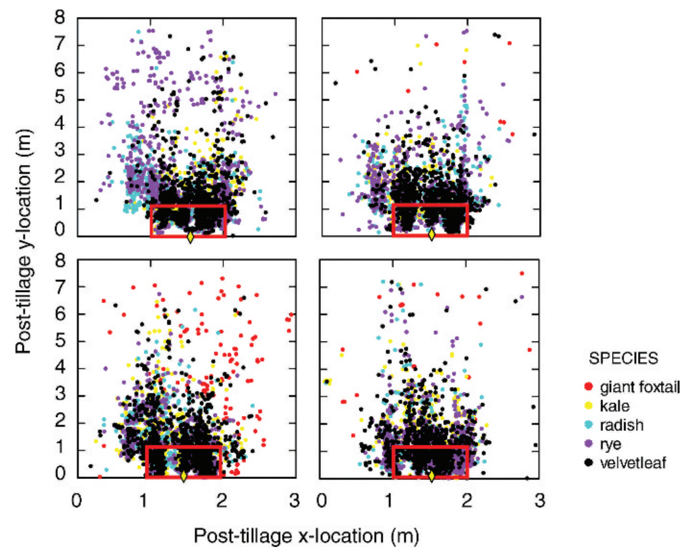

Figure 2. Digitized locations of synthetic seed bank species in Arlington, WI, April 2004, for all replications (replications 1 and 2, from left to right on top; replications 3 and 4, from left to right on bottom). Red rectangle indicates location of original 1-m^2 quadrat, whereas graph frame indicates relative position of expanded quadrat. Yellow diamond indicates origin of 1-m^2 quadrat, from which spatial displacement calculations were made. Tillage was performed perpendicular to the x-direction and parallel to the y-direction.

synthetic weed populations. A quadrat (i.e., a small area of ground with defined borders) is oversown with weed seeds of the study species and its boundaries are marked with seeds of a nondormant marker species. Tillage and planting operations deform the quadrat, moving both the weed and marker species, but these changes are measurable via the tracer species. This paper describes the procedure in detail and evaluates its effectiveness in tracking changes wrought by a single high disturbance event.

Materials and Methods

Field Study. Synthetic seed banks were established at the Michigan State University Crop and Soil Science Farm in East Lansing, MI, and at the University of Wisconsin Agronomy Farm in Arlington, WI, in April 2004. Soil types for these locations were, respectively, a Capac fine sandy loam (Fine-loamy, mixed, active, mesic Aquic Glossudalf; 2.1% organic carbon [OC] and pH of 7.3) and a Plano silt loam (fine silty, mixed mesic Typic Argiudoll; 4.1% OC and pH 5.8). Seed banks consisted of 1-m^2 quadrats sown with two weed (giant foxtail and velvetleaf) and three marker species ('Red Russian' kale, 'Cabernet' radish, and 'Wheeler' rye).[1] Marker species were chosen because their range in seed mass (4 mg seed^{-1}, 11.3 mg seed^{-1}, and 22.6 mg seed^{-1} for kale, radish, and rye, respectively) was similar to the range in seed mass of giant foxtail (2 mg seed^{-1}) and velvetleaf (9.5 mg seed^{-1}). At both locations, experimental sites were chosen that had received intensive weed management for the past 5 yr and had very low ambient populations of giant foxtail and velvetleaf (< 1 plant m^{-2}). Weed seeds were collected in the fall of 2003 along the margin of a no-till soybean [*Glycine max* (L.) Merr.] field in East Lansing, and stored in sealed polyethylene containers at 4 C until use. Tetrazolium testing (AOSA 2000) indicated that both seed lots had $> 90\%$ viability, with 80 and 22% mean dormancy for giant foxtail and velvetleaf, respectively. Seeds of both giant foxtail and velvetleaf were spread evenly over quadrats at a rate of 2,000 seeds m^{-2}, and lightly incorporated to a depth of 1 cm with a landscape rake. In the same quadrats, seeds of rye and radish were sown at 200 seeds m^{-1} of row into 1-cm-deep furrows made with the tip of a triangular onion hoe along the quadrat borders, whereas kale seeds were sown into the diagonals of each quadrat using the same method. Four quadrats were established at each experimental location, spaced at 25-m intervals along a 100-m transect.

The coordinates of each quadrat were recorded in relation to an external marker along the field margin, after which primary tillage and corn planting took place. Primary tillage was performed with a single pass, at a ground speed of 7 km hr^{-1}, of a soil finisher[2] comprised of concave disks, S-tine cultivators with sweeps, spike tooth harrows, and a rolling basket. Corn (*Zea mays* L.) was then planted in 76-cm rows parallel to the direction of tillage. Immediately following corn planting, quadrat corners were re-established and a 0.5-m grid was staked over a 3-m-wide expanded quadrat centered on the quadrat origin (Figures 1 and 2) and extending 8 m in the direction of tillage. Data on seedling emergence in Michigan was not collected in quadrats extending further than 4 m in the direction of tillage from the quadrat origin because no seedlings of marker species were found beyond this point, whereas seedlings of marker species were found up to 8 m from the quadrat origin in Wisconsin. This discrepancy may have been due to differences in soil type, soil conditions at the time of tillage, surface residue, or driving speed.

Ten d after the quadrats were established, images of study seedlings were recorded in the expanded quadrat. This time point was chosen to be late enough to allow all marker species to germinate, and for a first flush of recruitment from the sown weed seed populations, but early enough to avoid difficulty in distinguishing individuals due to subsequent growth. In Michigan, this procedure consisted of taking overlapping digital photographs of each grid tile within the expanded quadrat, at a resolution of 400 dots per inch (dpi), and from a height of 1.5 m. In Wisconsin, a tiled image of seedling locations in the expanded quadrat was obtained by use of a transparent plexiglass table covered with mylar transparencies, which were subsequently digitized using a flat bed scanner.

Image Processing. All images were imported into Adobe Photoshop CS Version 8.0,[3] after which they were ortho-rectified to remove distortions in the x-y coordinates arising from variable camera angle and distance from the subject. This was accomplished by using a skew transform to drag grid markers in the image to align with the rectilinear grid in the image processing software, and then saving the file as a 500 by 500 pixel bitmap. The rectified bitmaps were then joined into a composite image, saved as a 3,000 pixel wide by 4,000 pixel long (8,000 pixels long in Wisconsin) bitmap, corresponding to a 3,000 mm by 4,000 (8,000) mm expanded quadrat (Figures 1 and 2).

Composite images were then imported into ArcView 3.3[4] to obtain spatial coordinates for all study seedlings within each replication. A spatial layer was created for each species, with point markers placed over the center of each seedling. Once each species had a complete layer, x-y coordinates were obtained for all seedlings by using the "add x-y" subroutine, and exporting x-y attributes table as a text file.

Data Analysis. Seedling germination counts for each species were compared to numbers of seeds sown to obtain percent visual recovery of sown seeds. Seedling spatial distributions, defined as the number of seedlings that traveled a given distance from the origin binned in 10-cm increments, were determined for each species. To address the problem of whether weed seedlings were recruited from the experimental seed bank, as opposed to the ambient seed bank, we compared the spatial distributions of weed seedling displacement from the quadrat origin in the y-direction, parallel to tillage, with those of the boundary species, which had no ambient populations in the experimental locations. We reasoned that the spatial distribution, with respect to the original quadrat, of the boundary species and sown weeds would have a distinct signature in comparison to the natural weed populations, which would be expected to be randomly distributed with respect to the quadrat. No functional form was assumed for spatial distributions of marker and weed species. Instead, the nonparametric Kolmogorov-Smirnov two-sample statistic was used to test the null hypothesis that the empirical spatial distributions of weed and marker species did not differ (Conover 1980).

Evaluating the performance of marker species in tracking the movement of the sown weed species took place in two steps. First, we calculated the quantiles of movement of the marker species in the x- and y-directions, using seedling displacement from the quadrat origin as a measure of seed movement (for example, quantiles of movement for one replication of kale seedlings in Michigan are shown in Figure 3). Each quantile of marker species movement was then used to provide symmetrical x and y coordinates for a series of nested quadrats (Figure 3). Calculations for percent containment of weed species within each of the nested quadrats, a measure of how well the marker species was tracking movement of the sown nonmarker species, was then automated within MATLAB R2007a.[5] Observed values for

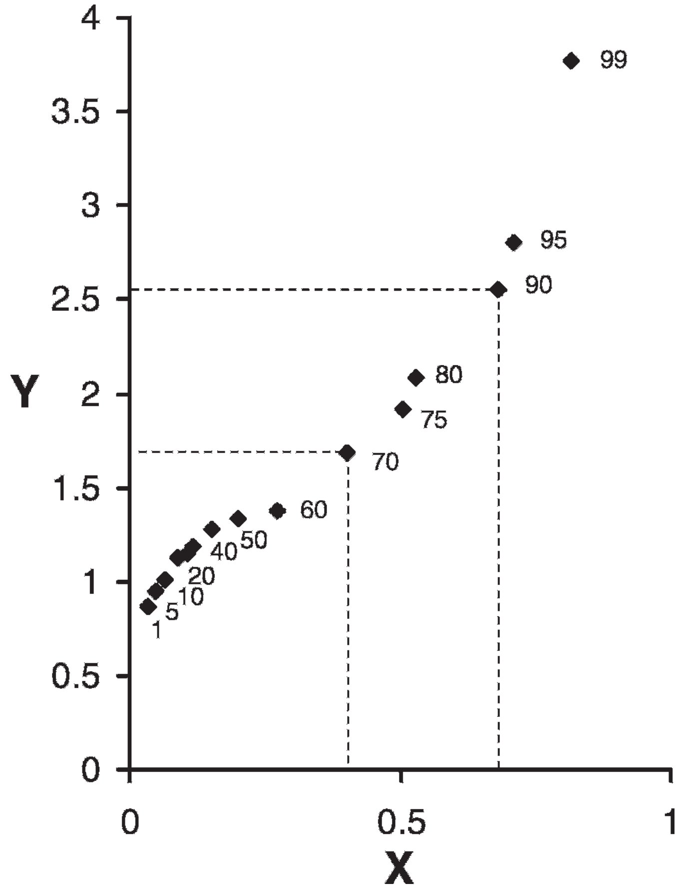

Figure 3. Empirical quantiles of movement perpendicular to (x), and parallel to (y), the direction of tillage for a single replication of the marker species kale in East Lansing, MI. Data labels indicate individual quantiles of movement. The figure represents one-half of a symmetrical distribution, with respect to the y-axis. Each quantile provided x and y coordinates for the corners of a series of nested quadrats (half-quadrats for 70th and 90th quantiles are shown with dotted lines) with which to measure percent containment of weed seedlings.

percent containment of weed species by marker species were compared against predicted values using a χ^2 test with 3 degrees of freedom (d.f.) (Conover 1980).

Skewness (g_1), the third central moment of the spatial distributions, was calculated using the following formula:

$$g_1 = \frac{1}{n\sigma^3}\sum_{i=1}^{n}(Yi - \bar{Y})^3 \qquad [1]$$

where n = number of observations, σ = standard deviation, Yi = value of individual observations, and Y = mean (Gotelli and Ellison 2004). Skewness is 0 in normal distributions, positive in right-skewed distributions, and negative in left-skewed distributions.

Results and Discussion

Seedling Maps. Maps of seedling positions indicated a close correspondence between marker and weed seed movement for most study species (Figures 1 and 2). This observation was supported by nonparametric comparisons of empirical seedling spatial distributions for marker and weed species (Table 1). Spatial distributions of all three marker species did not differ from those of velvetleaf in Michigan and Wisconsin or giant foxtail in Michigan. Since the marker species had

Table 1. Comparison of empirical spatial distributions of weed and marker species, in the direction of tillage. Studies were conducted in East Lansing, MI, and Arlington, WI.

Location	Replication	Giant foxtail			Velvetleaf		
		Kale	Radish	Rye	Kale	Radish	Rye
		P > T[a]					
MI	1	0.34	0.64	0.89	0.89	0.99	0.99
MI	2	0.16	0.31	0.89	0.89	0.99	0.89
MI	3	0.89	0.61	0.99	0.89	0.89	0.61
MI	4	0.61	0.89	0.89	0.61	0.99	0.99
WI	1	***	***	***	0.99	0.99	0.89
WI	2	**	*	*	0.99	0.99	0.99
WI	3	**	**	**	0.89	0.99	0.89
WI	4	***	***	***	0.99	0.99	0.89

[a] Nonparametric tests of the null hypothesis, that the empirical spatial distribution functions of the weed and marker species did not differ, were conducted within replications using the Kolmogorov-Smirnov statistic T. The symbols *, **, and *** represent rejection of the null hypothesis at α levels 0.05, 0.01, and 0.001, respectively.

been sown deliberately, with no chance of background contamination from an ambient seed bank, this result indicated that weed seedling germination in these quadrats was primarily from sown populations. The spatial distribution of giant foxtail seedlings in Wisconsin, however, was significantly different from those of all three marker species (Table 1). Whereas all other species in the study showed unimodal, right-skewed spatial distributions (g_1 ranging from 0.34 to 3.2), giant foxtail seedlings in Wisconsin followed a uniform distribution (Kolmogorov-Smirnov test for difference between giant foxtail empirical distribution and uniform distribution: $P = 0.17$). This finding suggests that giant foxtail seedling recruitment in Wisconsin (Table 2) came mostly from the ambient seed bank rather than from sown seeds. A single tillage operation disturbing a sown patch of seeds will necessarily leave a right-skewed spatial distribution of the seeds, since the tillage equipment moves through, and then away from, the seed source. If tillage were to continue in both directions over several seasons, the spatial signal of the original pulse of seeds would be flattened out to form a uniform distribution. Additional evidence supporting this assertion is that seedling recruitment was greater for all species in Wisconsin than in Michigan ($P < 0.05$), with the exception of giant foxtail, which had very low germination in Wisconsin. Low levels of seedling recruitment of all study species in Michigan (Table 2) was likely due to heavy rains and saturated soils in the 10 d period following sowing and tillage. Lack of dormancy in the marker species resulted in their recruitment and growth, even in wet soils. To avoid obscuring differences between individuals due to continued growth and expansion of true leaves, we made the decision to mark seedling locations at the 10-d interval despite low overall recruitment rates.

Table 2. Recruitment of seeds from synthetic seed banks in East Lansing, MI, and Arlington, WI, in April 2004.

Species	Seedling recruitment	
	MI	WI
	%	
Giant foxtail	9 (0.7)[a]	1.8 (1.7)
Velvetleaf	11 (2.1)	65 (1.8)
Kale	13 (1.2)	86 (7.4)
Radish	29 (1.1)	91 (3.5)
Rye	31 (1.4)	75 (9.3)

[a] Values represent mean and standard error of four replications, within locations.

Evaluation of Living Boundaries Method. Percent containment of weed seedlings by marker species was positively associated with marker species movement for velvetleaf in Michigan and Wisconsin, and giant foxtail in Michigan, with coefficients of correlation between these two variables ranging from 0.90 to 0.99 ($P < 0.01$). For each of these species/location combinations, the correspondence between weed and marker species improved at higher quantiles of marker species movement (Figure 4). Marker species containment of weed seedlings reached 100% at the 50th, 90th, and 95th quantiles of marker species movement for velvetleaf in Wisconsin, velvetleaf in Michigan, and giant foxtail in Michigan, respectively. Containment of giant foxtail in Wisconsin by all three marker species was poor ($\leq$ 20%), presumably due to the confounding of ambient and sown seeds in this case.

We also examined the proportion of giant foxtail and velvetleaf seedlings that emerged within the original quadrat boundaries during the study period, compared to those emerging outside of those boundaries. For both weed species, a large proportion of seedlings emerged outside of the original quadrat boundaries, indicating that tillage had displaced many of the seeds horizontally. In Michigan and Wisconsin, 24 and 25% of giant foxtail seedlings, and 52 and 40% of velvetleaf seedlings, respectively, emerged within the original quadrat boundaries. Between 50 and 75% of the original study seeds appear to have been moved outside of the original quadrat by tillage. This represents a conservative estimate of the amount of seed movement that could occur in a system receiving multiple soil disturbance operations.

These results provide useful feedback about the living boundaries method. First, the problem of noise from ambient weed seed banks obscuring signals from sown seeds cannot be ignored. In situations with high background seed populations of target species, the answer is to enrich the proportion of seeds arising from sown seeds relative to ambient seeds. Potential solutions to this problem include sowing experimental seeds at rates much higher than observed seed bank density ranges, and to increase germination rates of sown seeds by stratifying them, either overwinter under field conditions or using laboratory methods for breaking dormancy (Buhler and Hoffman 1999). Second, the position of marker species, relative to the original quadrat, did not have an appreciable impact on the results: sowing quadrat boundaries and diagonals worked equally well. Clearly the amount of soil "mixing" that occurred is large relative to distribution of initial distances between seeds of marker and test species. Third, although we chose three marker species differing in

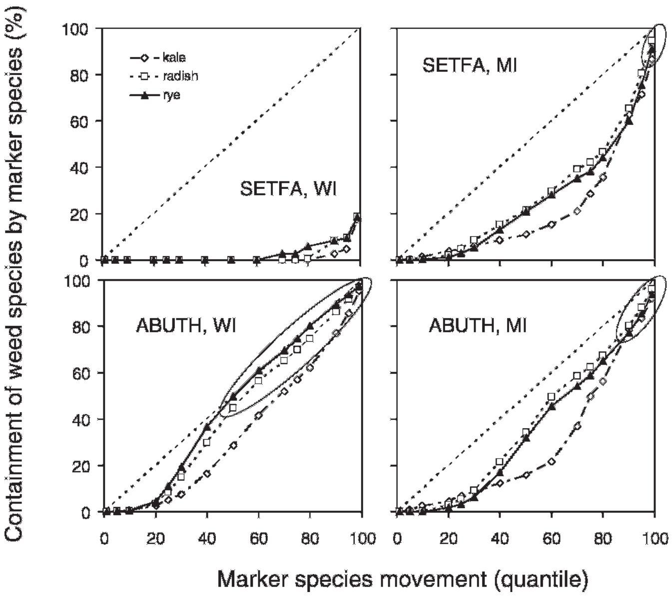

Figure 4. Percent containment of sown giant foxtail (SETFA) and velvetleaf (ABUTH) seedlings within nested quadrats corresponding to quantiles of movement for the marker species kale, radish, and rye in East Lansing, MI, and Arlington, WI. The ellipses denote data points for which percent containment of weed seedlings by marker species was not significantly different, at $\alpha = 0.05$, from expected containment (dotted 1 : 1 line) if the marker species were tracking quantiles of movement of the weed seeds, based on a χ^2 test with 3 degrees of freedom (d.f.).

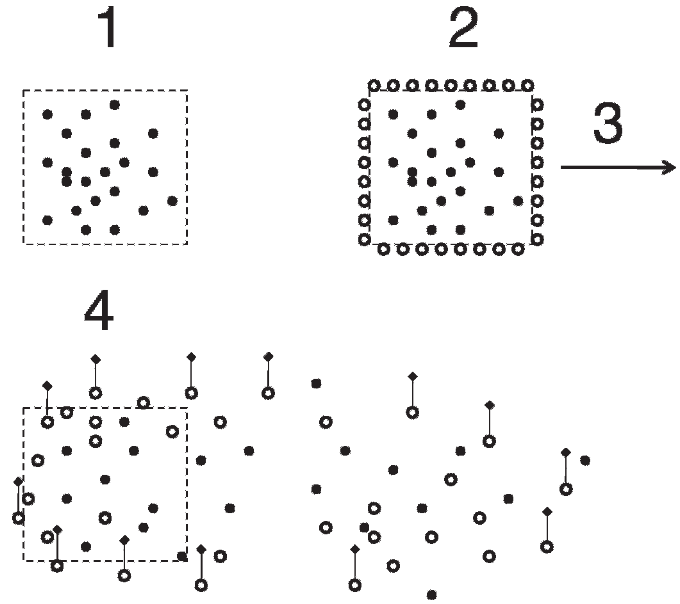

Figure 5. The "living boundaries" approach to tracking weed seeds in situ for demographic studies subjected to soil disturbance. Step 1: Sow seeds of study weed species (solid circles) within a defined quadrat (dotted line). Seeds should be characterized for dormancy and viability, and the study area should have a low ambient soil seed bank for this species. Step 2: Sow seeds of nondormant crop species (open circles) with similar seed mass to study species along borders of quadrat. Step 3: Perform tillage and plant. Step 4: After marker species have emerged, flag (diamond-headed vertical lines) the convex hull connecting the outermost seedlings of the marker species in the new, expanded quadrat. This flagged area contains close to all of the sown weed species.

mass, with the idea that marker species would track more closely those weed species whose mass they were closest to, there was no difference in the ability of the three marker species to track either weed species (Figure 4). Finally, the living boundaries method appears to provide a robust method for tracking sown quadrats, given the above caveats. When quadrats are sown to mimic natural seed dispersal schedules (e.g., fall-sown quadrats for summer annual species), nondormant boundary species can be sown immediately prior to agronomic operations. Since percent containment of weed seeds by marker species was 100% at the 99th quantile for all species/site combinations where weed seedlings represented the sown population (Table 1; Figure 4), this suggests a simple rule for applying the method to demography experiments: after the original quadrat is deformed and seedlings have emerged, flag the polygon containing all marker seedlings (i.e., the convex hull) to obtain the expanded quadrat containing the study weed population (Figure 5). We did not collect data to determine whether the method could be of use to longer-term cropping system studies, but potentially, the flagged convex hull could be resown with marker species the following spring, and the whole process repeated.

We believe the method has several advantages over previous methods. In comparison to synthetic seed banks with artificial boundaries, the living boundaries approach allows for agronomic operations to be applied to the system in a normal manner, yet still maintains clear spatial boundaries for the study quadrat. In contrast to unbounded large-scale synthetic seed banks, the living boundaries approach allows the experimenter to follow changes in study population numbers with good precision. As shown by the large proportion of seedlings emerging outside of the original quadrat, a seed bank study that only used a fixed quadrat to follow seed bank dynamics in a tilled system would not be able to follow the fates of 50 to 75% of the experimental seeds. Finally, unlike a sown-bead study (Mohler et al. 2006), in which precise estimates of the effects of agronomic operations on seed dispersal are obtained, but seed dispersal is uncoupled from demography, the present method allows spatial dispersal and within-season demography to be studied in parallel.

Sources of Materials

[1] Johnny's Selected Seeds, 955 Benton Ave., Winslow, ME 04901.

[2] Sunflower 6200 Soil Finisher, 3154 Hallie Trail, Box 566, Beloit, KS 67420.

[3] Adobe Systems Incorporated, 345 Park Avenue, San Jose, CA 95110.

[4] ESRI Software, 380 New York Street, Redlands, CA 92373.

[5] The MathWorks, Inc., 3 Apple Hill Drive, Natick, MA 01760.

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